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Bionomics of the four-eyed spruce bark beetle, *Polygraphus rufipennis* (Kirby) (Col., Scolytidae) in Newfoundland II. Host colonization sequence

W. W. Bowers, J. H. Borden and A. G. Raske
Natural Resources Canada - Canadian Forest Service, St. John's, Newfoundland

Abstract: The four-eyed spruce bark beetle, *P. rufipennis*, is a phloeophagous bark beetle restricted to Abietineae hosts in northern and mountainous area of North America. Projected wood shortages in Newfoundland have focused attention on the bark beetle and its role in contributing to black spruce mortality. Our findings disclosed that colonization on felled and standing trees by *P. rufipennis* followed the typical host selection sequence of scolytids, notably, emergence, dispersal, selection and establishment. All brood stages except eggs overwintered in black spruce, however, the majority of overwintering stadia consisted of larvae and callow adults. Adult mortality was significant during winter, especially in standing severed and felled trees. In Newfoundland, *P. rufipennis* had 1 generation and produced a spring and summer brood. Four weeks after establishing a first brood, parent adults re-emerged to establish a second brood. Development from egg to adult took ≈2 months. *P. rufipennis* of either sex initiated attack at mean densities per 100 cm^2 of 8.1 and 9.3 on felled and standing-severed trees, respectively. Densities were significantly lower at 4.7 per 100 cm^2 on standing unsevered trees. Following copulation, males stayed with the females and exhibit guarding behaviour by occupying the entrance hole. Significantly higher numbers of galleries were established on trees felled in shade than in full sunlight. Black spruce attacked by *P. rufipennis* were often secondarily attacked by *Dryocoetes affaber* and *Crypturgus borealis*. Other associates included *Medetera* sp. and the cylindrical bark beetle, *L. intricatus*.

1 Introduction

The four-eyed spruce bark beetle, *Polygraphus rufipennis* (Kirby) is found throughout the northern coniferous forest from Alaska to Newfoundland and the northern and mountainous parts of the United States (Bright, 1976; Wood, 1982). The insect is reported to attack all conifers in its range, but prefers *Picea* spp. (Hopkins 1899; Blackman and Stage, 1918; Simpson, 1929; Hilton, 1968).

P. rufipennis usually feeds on recently broken, cut, or fallen trees. However, the presence of large numbers of weakened trees can result in outbreak populations that kill large quantities of timber, especially black spruce, *Picea mariana* (Mill.) B.S.P. (Swaine, 1918). From 1882 to 1893 in West Virginia and in New York state, widespread mortality of red spruce, *Picea rubens* Sarg., occurred following attack by *P. rufipennis* (Hopkins 1899; Blackman and Stage, 1918). Mielke et al. (1986) reported large numbers of dead and dying red spruce attacked by *P. rufipennis* in West Virginia. Similarly, the closely related European species, *Polygraphus poligraphus* L., can reach outbreak levels following disturbance of spruce stands (Chrystal, 1949; Lekander, 1959).

An outbreak of the eastern spruce budworm, *Choristoneura fumiferana* (Clem.), on *P. mariana* began in 1972 in Newfoundland and collapsed in most stands by 1984. Coincident with an increase in populations of *P. rufipennis*, sudden spruce mortality was first detected in the fall of 1982 and occurred over 81 000 ha with a loss of 2 002 000 m^3 of black spruce (Raske and Sutton, 1986). The area affected had increased to 95 700 ha with dead volume of 3 194 000 m^3 by the end of 1983 (table 1). The awareness that these stands may be predisposed to attack by *P. rufipennis* resulted in a corresponding awareness of the lack of information concerning the beetle's bionomics in Newfoundland. The present paper describes the host colonization sequence of *P. rufipennis*. Results relating to emergence and flight patterns are reported seperately (Bowers et al., 1996).

2 Materials and methods

2.1 General

Except where otherwise noted, research was conducted near Miguels Lake in the northwestern part of the Gander River

Table 1. *Cumulative areas and volumes of dead and severely damaged black spruce in areas of more than 10% tree mortality in Newfoundland from 1977 to 1983*

Year	Area (ha)	Volume (m^3) Severely damaged	Dead	Total stand
1977	12 000	600	18 000	—
1978	19 000	7 000	57 000	—
1979	49 000	26 000	216 000	—
1980	66 000	150 000	420 000	—
1981	67 000	78 000	507 000	—
1982	81 000	464 000	2 002 000	8 233 000
1983	95 700	915 000	3 194 000	10 322 000

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watershed (55 32'30"W longitude, 48 41'35"N latitude). The watershed is dominated by 7–14 m high, 120-year-old black spruce, which had been severely defoliated by eastern spruce budworm. White birch, *Betula papyrifera* Marsh., trembling aspen, *Populus tremuloides* Michx., and balsam fir, *Abies balsamea* (L.) Mill., occurred sporadically in forest stands at the study site. Understory vegetation was dominated by northern sheep laurel, *Kalmia angustifolia* L.

2.2 Colonization sequence of *P. rufipennis*

2.2.1 Overwintering site and stadia

On 26 May, 1983 six 5 l duff samples were collected from the base of six black spruce trees killed in 1982 by *P. rufipennis*. Samples were maintained indoors at room temperature in Styrofoam® emergence containers until 1 July. Each container measured 30.5 × 35.6 × 20.3 cm and was fitted with a glass vial to capture emerging adult beetles. Emergence was checked daily during the first 2 weeks of the study and weekly thereafter. In December, 1983, six additional duff samples were collected from beneath six trees attacked the previous summer. Samples were maintained in emergence containers at room temperature until 30 April, 1984. Emergence was checked weekly for the four-month period.

Observations were made in May, 1983 to identify the overwintering stages of *P. rufipennis* exposed in slices of bark removed from the bole of six black spruce trees at breast height (1.3 m). Also, on 13 December, 1983 one 100 cm^2 bark sample was examined from each of four black spruces infested by *P. rufipennis*. To compare within-tree brood survival before and after winter, bark samples were removed with a 100 cm^2 bark punch (Furniss, 1962) in the fall of 1983 from seven felled trees and from seven standing severed trees and three standing unsevered trees. Seven of the felled trees were sampled at 0.5, 2.0, 3.5 and 5.0 m from the base and six trees were sampled at 0.5, 2.0 and 3.5 m from the base. On standing trees, bark samples were removed at breast height. Counts of live and dead callow adults were made to estimate survival per gallery. Sampling was repeated in the spring of 1984. The Pearson χ^2 test of independence (Zar, 1984) was used to test the null hypothesis that the frequency of surviving callow adults was independent of overwintering conditions. In this and in all subsequent tests $\alpha = 0.05$.

2.2.2 Host selection, attack and brood establishment

Seventeen black spruce were girdled at a height of 0.5 m by removing a 10 cm-wide band of bark. Ten trees (x̄d.b.h. = 13.9 cm) (d.b.h. = diameter at breast height) were girdled during 24–30 May, at the beginning of flight in 1983, and seven trees (x̄dhh = 13.4 cm) were girdled during the first week of July, at the start of parent adult re-emergence. The 10 trees were monitored for attack biweekly, and at the end of the summer flight 100 cm^2 bark samples were taken from the east aspect at 0.5, 2.0, 3.5 and 5.0 m heights from three spring attacked trees to determine the number of galleries successfully established by *P. rufipennis*. Twenty trees were also girdled on 20 June, 1984, 6 days following the first attack by emerging spring brood. Three trees successfully attacked by 4 July were used to study parent adult re-emergence; two bark samples were removed at breast height from the remaining 17 trees on 12 September to determine the number of girdled trees successfully colonized.

Attacking beetles were observed for several hours on the evening of 31 May, 1983 as they walked on and bored into bark tissue of two adjacent black spruce trees severely damaged by spruce budworm. At each of 20 newly established attack sites, the bark circumscribing the attack was excised and the number and sex of attacking adults determined.

On 18 May, 1983 three black spruce trees 10–15 m apart were selected in each of 10 groups spaced 25 m apart. Within each group one tree was left standing, one was felled and one was secured upright with rope, severed at 0.5 m from the base, and a plastic-covered wooden board was placed in the saw kerf to prevent translocation. Nails were driven through the stem at the kerf to provide additional support. Each tree was checked daily until attack occurred and twice weekly thereafter. One week following attack, 100 cm^2 bark samples were taken from east and west aspects at breast height from standing severed trees, and at 0.5, 2.0, 3.5 and 5.0 m from standing unsevered trees to determine the number of *P. rufipennis* entrance holes, nuptial chambers and galleries. West and east aspect samples were pooled prior to analysis. Felled trees were sampled along the lateral aspects of the bole at 0.5, 2.0, 3.5 and 5.0 m from the base. Bark samples were placed into petri dishes, sealed with tape, labelled, and returned to the laboratory for dissection. Samples were examined immediately or after storage at 8–10 C for up to 2 days. Galleries intersected at the edge of samples were examined for life stages, and counted but not measured. Adult beetles were sexed, counted and preserved in 70% ethanol, as were all larvae and pupae. Representative specimens of *P. rufipennis* and its associates were also pinned for subsequent identification. The height, diameter and bark thickness at each sample height of each tree was recorded.

The pattern of gallery construction and relationships between the number of egg niches, eggs and length of gallery arms (female tunnels) were derived from 284 intact galleries pooled from all sampled trees. Only egg niches from which a larval mine ensued were counted as an oviposited egg.

After the spring flight the bark of most trees became severely desiccated, and attack by *Dryocoetes affaber* (Mannerheim) and *Crypturgus borealis* Swaine, obscured many *P. rufipennis* galleries. Therefore, beginning in July, the number of galleries per bark sample established by *P. rufipennis* was examined and quantified only from bark samples without multiple infestations.

Three experiments (Exp. 1–3) were initiated in 1984 to investigate the seasonal life history of *P. rufipennis*. In Exp. 1, 10 black spruce trees were felled on 30 May. All were attacked by the third week of June and 100 cm^2 bark samples were removed from the mid-bole and base of 7 trees on 11 July and from the mid- bole and base of 4 trees on 2, 12, 22, and 29 August, and on 7 and 12 September. In the 62 bark samples 131 intact female tunnels were measured and the number of egg niches and developing brood counted. At the start of re-emergence on 10 July, more trees were felled adjacent to spring-attacked trees to test whether emerging parent adults could establish a second brood. Bark samples were first removed from these trees at mid-bole and at the base 2 weeks following attack on 2 August, and again on 12, 22, and 29 August, and on 7 and 12 September. Ninety-two female tunnels were measured and the number of egg niches and developing brood determined. Also, two second brood trees were each fitted with four emergence traps to test for parent adult re-emergence. To test for possible third brood establishment by these parents, four additional trees were felled on 20 August and sampled on 12 September as above.

Exp. 2 utilized parent beetles obtained by peeling bark from three trees infested in spring 1984 and removing them from their galleries. Five fresh bolts infested with 50 male and 50 females of these parents and wrapped with Saran screening to protect against further attack were left on the forest floor from 11 July to 23 August to test for a second *P. rufipennis* brood. bark was peeled from the bolts, female tunnels were measured and the numbers of egg niches and life-stages quantified.

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Twenty pairs of parent adults recovered from these bolts were placed on each of three, 1 m long fresh black spruce bolts, which were left in the field from 23 August to 13 September, and examined as above for evidence of a third brood.

Exp. 3 used brood adults retrieved from girdled trees attacked during July, 1983. These adults presumably overwintered as larvae and represented the second-brood progeny of re-emerged parents in 1983. Three 1 m long fresh bolts each infested with 40 pairs of *P. rufipennis* were left in the field from 11 July to 23 August, and then examined as above. Finally, 10 pairs of parent adults recovered from these logs were placed on each of two, 1 m long fresh logs and placed in the field from 23 August to 13 September to test as above for a second brood.

Descriptive statistics used to describe colonization patterns on black spruce, including the number of entrance holes, nuptial chambers and galleries, were derived using SAS (1985) procedures. The cumulative number of beetle attacks over time was described by fitting a smoothed curve using a spline plot (SIGMAPLOT, 1991). Female tunnel length, was regressed against time, and the linear associations between egg niche and tunnel length, egg and tunnel length, and egg and egg niche, were estimated (SAS, 1985).

2.2.3 Parent adult re-emergence

Standing-severed black spruce trees attacked by *P. rufipennis* in spring were fitted on 1 July 1983 with 100 cm^2 emergence traps placed at breast height on the west aspect of five trees and on the east aspect of five trees. These 10 trees were checked to ensure that re-emergence had not started prior to trap attachment. Each collecting vial contained a small strip of paper on which the emerged beetles could crawl. Beetles were collected weekly, counted, sexed, and placed on caged fresh spruce bolts at room temperature. After the appearance of copious amounts of frass on the bolts, a fresh spruce bolt was added to each cage to allow re-emergent parents to establish a third brood. To determine which sex of re-emergent beetles initiates attack, two cages were set up with males and females, one with only males and one with only females. Near the end of the study season, these bolts were debarked and examined for successful attacks. Re-emergence was also evaluated in 1984 using on-tree emergence traps placed at breast height on the east and west aspects of five trees. Three of these trees had been girdled in spring to initiate attack.

2.3 Host colonization under sun and shade

The colonization sequence of *P. rufipennis* in sun and shade was investigated at five locations within the Miguels Lake watershed. Five healthy black spruce trees of similar height and diameter were felled at location 1 on 20 May and at locations 2 and 3 on 26 May, 1983. Each of the 15 trees was cut in half at mid-bole, and one-half was randomly selected and placed in a shaded understory while the other half was placed in a clearing exposed to full sunlight. Branches were left intact on all trees and each tree bole was inspected weekly. Three bark samples (100 cm^2) were removed on 15 August from the side of each bole section, at positions corresponding to *c.* 33, 50 and 67% of the total lengths, and examined for egg galleries and brood adults.

One on-tree emergence trap was placed at each of the three sample positions on one tree in sun and one tree in shade at two locations on 30 May, 1984. The 12 emergence traps were removed on 4 July, and emerged adults were collected and counted. Also, five trees were felled at each of two more locations on 5 and 13 June 1984 and the sun and shade treatment repeated. Bark samples for examination as above were removed from these trees at midbole from the upper, side and bottom aspects on 18 July at one location and on 24 July at the other. A two-way analysis of variance was used to determine how position along the bole or aspect in combination with light exposure affected gallery establishment. In 1984, 40 intact egg galleries established on the lateral aspects of trees felled in sun and shade were dissected to determine mean gallery length. Data were screened for distributional form and analysed using BMDP statistical procedures (DIXON, 1988).

2.4 Insect associates

Soon after attack by the four-eyed spruce beetle trees often were invaded by *D. affaber* and *C. borealis*. Adults of these species were collected from bark tissue as described above, sexed, and preserved in 70% ethanol. Representative specimens were pinned for subsequent identification.

3 Results

3.1 Colonization sequence of *P. rufipennis*

3.1.1 Overwintering site and stadia

No *P. rufipennis* emerged from duff collected in spring or winter, 1983. Examination of bark in spring 1983 disclosed all brood stages except eggs, the majority consisting of overwintering callow adults. Winter bark samples in 1983 revealed overwintering larvae ($\bar{x} \pm SE = 16.8 \pm 9.7/100\,cm^2$, $N = 4$) and callow adults ($17.3 \pm 9.9/100\,cm^2$, $N = 4$) of *P. rufipennis*. Significant mortality of overwintering adults occurred in standing severed black spruce trees and at all positions along the bole of felled trees, but not in standing unsevered trees. (fig. 1).

3.1.2 Host selection, attack and brood establishment

During the spring flight in 1983, one of 10 girdled black spruce trees was attacked by *P. rufipennis*. Fresh frass and entrance holes were observed ≈ 10 days after the tree was girdled; no attack was evident above 2 m on the tree bole. Five of seven trees girdled at the beginning of parent adult re-emergence were attacked in summer, all within 2 weeks after girdling. Bark samples removed on 16 August from three attacked trees disclosed nine galleries at 0.5 m on one tree and four galleries at each of 0.5 and 2.0 m heights on a second tree. No evidence of successful gallery establishment was found on the third tree even though frass was apparent on the bark. Seven of 20 girdled trees were successfully colonized by *P. rufipennis* in 1984. Dissection of bark samples on 12 September disclosed developing larvae and callow adults.

P. rufipennis initiated attacks under bark scales and on exposed areas of bark. Nine of 20 attack sites established on two standing green trees in spring 1983 had entrance holes occupied by a lone male. At seven attack sites nuptial chambers had been formed; four chambers were occupied by one male, and three chambers were occupied by one male and one female. Initiation of egg tunnels had commenced in the remaining four galleries, three occupied by one male and two females and one by three females.

P. rufipennis colonized two standing unsevered trees, 10 standing severed and seven felled trees during 1983 (table 2). The mean interval between treatment and

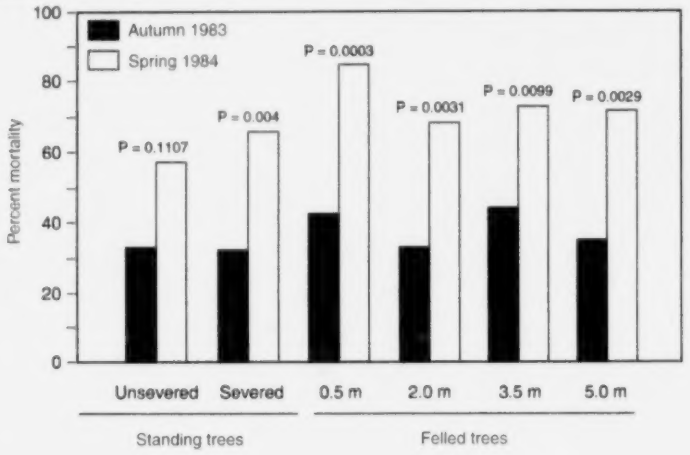

Fig. 1. *Mortality of* P. rufipennis *adults observed at breast height in standing black spruce trees and 0.5, 2.0, 3.5 and 5.0 m from the base of felled black spruce trees before and after winter, 1983–84. Probabilities above paired bars indicate differences in mortality before and after winter (χ^2 test)*

attack was approximately two weeks for standing trees and nearly four weeks for felled trees. Similarly, the interval between first emergence and first attack was three weeks for felled trees, and < 2 weeks for standing trees.

No significant difference in the overall mean number of attacks per 100 cm^2 was observed between felled (8.1 ± 0.92, N = 44) and standing severed (9.3 ± 1.2, N = 28) trees. However, significantly fewer attacks (4.7 ± 0.80, N = 28) occurred on standing unsevered trees than on felled or standing severed trees. Moreover, the number of attacks following initial attack in spring, increased considerably faster on felled and standing severed trees than on standing unsevered trees (fig. 2).

The number of attacks at each of four positions along the bole was consistently, but not significantly (*t*-test, $P \geq 0.05$) lower on standing unsevered than on felled trees (fig. 3). No linear regression function described adequately the relationship between either sample position or bark thickness and the mean number of attacks for felled or for standing unsevered trees. Construction of nuptial chambers and female tunnels (egg galleries) began within seven days following attack on felled and standing severed trees (fig. 4). On standing unsevered trees, no nuptial chambers or parental tunnels were observed one week following attack. Beetles of either sex apparently initiated attacks, although most attacks and nuptial chambers were initiated by males (table 3).

The majority of early attacks in spring, 1983 were characterized by one or two egg galleries (fig. 5). Attacks with one egg gallery accounted for 67.4, 52.0 and 44.6% of the total galleries on felled, standing severed and standing unsevered trees, respectively. Two attacks with six egg galleries were found in bark samples from standing severed trees. Fully formed gallery systems were of the radiate type (CHAMBERLIN, 1939, 1958), with 2–6 egg galleries joined to a large central nuptial chamber. The length of egg galleries increased linearly, but weakly, with time up to 5 weeks following first attack, when the mean length was 16.8 mm ($Y = 2.4 + 2.3X$, $P < 0.001$, $r^2 = 0.346$).

Analysis of brood production in spring, 1983, disclosed significant linear associations between the number of egg niches established by female *P. rufipennis* and egg gallery length ($Y = -1.7 + 0.5X$, $P < 0.0001$, $r^2 = 0.582$) between number of eggs and tunnel length ($Y = -1.1 + 0.4X$, $P < 0.0001$, $r^2 = 0.460$), and between the number of eggs and the number of egg niches ($y = 0.24 + 0.7X$, $P < 0.0001$, $r^2 = 0.620$). The average number of egg niches per mm of egg gallery was 0.37. With an increase in the number of egg galleries per gallery system, there were concomitant increases in the numbers of eggs niches and eggs per gallery system (fig. 6). With an increase in the number of egg galleries per gallery system, there also was an increase in the female to male sex ratio.

In spring 1984 *P. rufipennis* had established a first brood on felled black spruce approximately 1 week after the start of emergence. One month later, eggs and larvae comprised 58.7 and 41.3% of the total brood, respectively (fig. 7). Two months following attack, larvae and pupae represented 65.8 and 20.8% of the brood, respec-

Table 2. *Colonization of standing unsevered, standing severed, and felled black spruce by* P. rufipennis *Newfoundland, 1983*

	dbh ($\bar{x} \pm$SE)	Height ($\bar{x} \pm$SE)	No. of trees attacked spring	No. of trees attacked summer	Mean ($\pm$SE) number of days[a] treatment attack	Mean ($\pm$SE) number of days[b] emergence attack
Felled	10.5 ± 0.5	8.9 ± 0.5	4	3	27.5 ± 4.9	21.8 ± 4.8
Standing severed	10.2 ± 0.7	9.1 ± 0.5	7	3	16.0 ± 1.2	11.4 ± 1.3
Standing unsevered	11.6 ± 0.5	10.3 ± 0.8	2	0	13.0 ± 6.0	9.0 ± 6.0

[a] Mean time intervals determined for trees attacked in spring.
[b] Emergence first observed on 23 May.

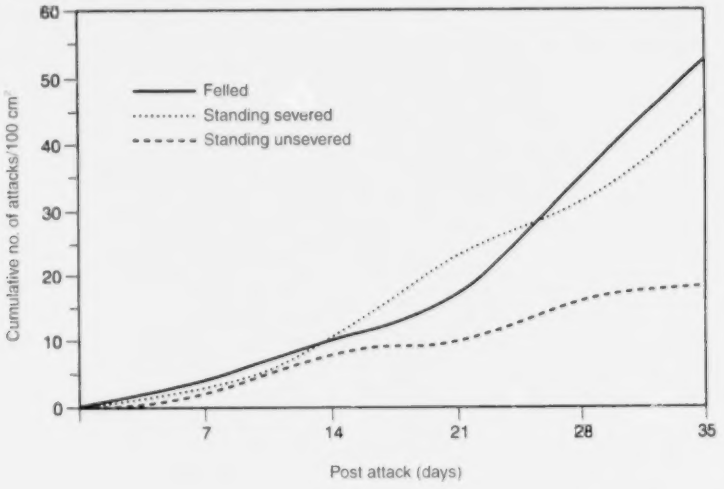

Fig. 2. *Cumulative number of attacks by* P. rufipennis *on felled (N = 4), standing severed (N = 7), and standing unsevered (N = 2) black spruce, 1983. Bark samples with multiple infestations excluded from the analysis*

tively. Callow adults were first observed on 22 August, when they accounted for 18.9% of the brood. At the beginning of fall, the proportions of larvae, pupae and callow adults were 53.3, 35.6 and 11.1%, respectively. Re-emerged parent adults established a second (summer) brood on felled trees during the third week of July, 1984. Two weeks later, eggs and larvae comprised 65.3 and 39.5% of the total brood, respectively (fig. 7). Pupae accounted for 4.8% of the brood, and no callow adults were present by 6 September, 55 days following initial attack. There was little evidence for a third brood in 1984. Only one parent adult *P. rufipennis* reemerged from two summer brood trees fitted with emergence traps on 7 August. Moreover, 16 galleries established on trees felled on 20 August contained only eggs and early stage larvae on 29 August and 12 September.

The mean lengths of egg galleries established for first (spring) and second (summer) broods by females in 1984 (table 4, Exp. 1) were nearly identical to those for the first brood in 1983. Furthermore, the mean number of egg niches per mm of gallery length varied little among broods in 1984 (table 4, Exp. 1), and was only slightly higher than for 1983. The linear associations between

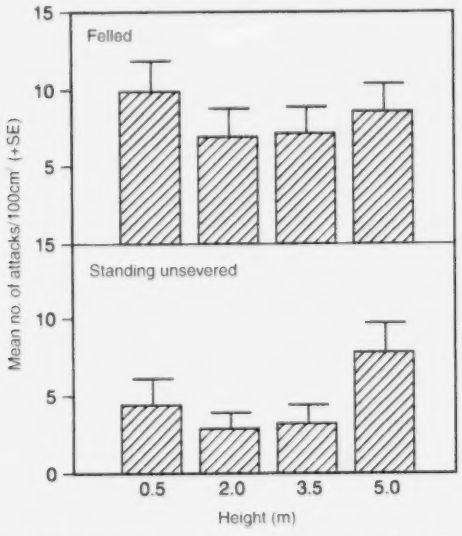

Fig. 3. *Mean number of attacks per 100 cm² by* P. rufipennis *at four positions along the bole of felled (N = 44) and standing unsevered (N = 28) black spruce, spring 1983*

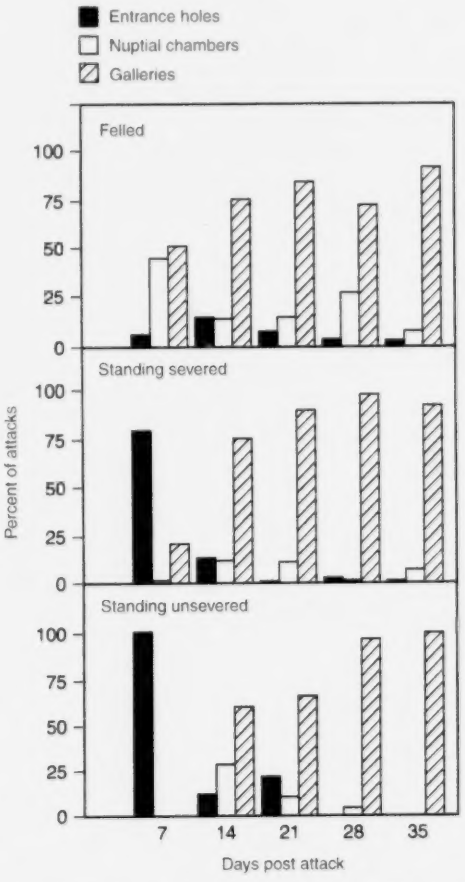

Fig. 4. *Proportion of entrance holes, nuptial chambers and egg galleries in felled, standing severed, and standing unsevered trees following attack by* P. rufipennis *in spring 1983*

Table 3. *Number of entrance holes and nuptial chambers occupied by male and female* P. rufipennis *attacking black spruce in Newfoundland, 1983*

Sex present[a]	Entrance holes	Nuptial chambers
None	7	2
1 ♀	25	42
1 ♂	14	22
2	1	3
1 ♀+1 ♂	2	22
1 ♀+2 ♂	0	6
1 ♀+3 ♂	0	3
	49	100

[a]Occupancy determined for attacking brood on 13 trees attacked in spring

the numbers of egg niches and lengths of egg galleries for the 1984 spring and summer broods ($Y = 0.4 + 0.5X$, $P < 0.0001$, $r^2 = 0.540$) and ($Y = 1.2 + 0.4X$, $P < 0.0001$, $r^2 = 0.620$, respectively) were nearly identical to those for the 1983 spring brood. In contrast, the linear association between the numbers of eggs and lengths of egg galleries observed in spring, 1984 ($Y = 1.8 + 0.2X$, $P < 0.008$, $r^2 = 0.080$) was weaker than that observed in summer, 1984 ($Y = 0.4 + 0.3X$, $P < 0.0001$, $r^2 = 0.370$), and weaker than that previously observed in spring, 1983. Likewise, a slightly weaker association between eggs and egg niches was evident in spring 1984 ($Y = 0.4 + 0.6X$, $P < 0.0001$, $r^2 = 0.0.430$) than in summer, 1984 ($Y = -0.8 + 0.7X$, $P < 0.0001$, $r^2 = 0.580$) and in spring, 1983.

Samples removed from trees felled to test for the possibility of a third brood revealed only 16 egg galleries with 74 egg niches containing 48 eggs. The mean egg gallery length and the mean number of egg niches were reduced by ≈ 50% from those in the spring, but the number of egg niches per mm of gallery length was consistent with the numbers produced in spring and summer (table 4, Exp. 1).

Brood establishment on bolts artificially infested with parent *P. rufipennis* confirmed that re-emerged adults are capable of producing a second, and possibly a third, brood in Newfoundland. Thirty gallery systems ($\bar{x}$ length of egg galleries = 18.7 ± 1.4) were established on second brood logs 44 days following infestation in summer 1984 and 10 gallery systems ($\bar{x}$ length of egg galleries = 9.1 ± 1.2) were established on 3 third brood logs, 21 days following infestation, in fall, 1984 (table 4, Exp. 2). The mean number of egg niches established in second and third brood logs artificially infested with parent adults differed little from the numbers established in natural infestations. Second brood eggs, larvae and pupae accounted for 3.1, 93.8 and 3.1% of the total brood, respectively. Eggs and larvae constituted 58.8 and 41.2% of the third brood, respectively.

Parent adults that presumably overwintered as late instar larvae and were artificially introduced into logs in summer, 1984 produced a first brood comprised of 5.6% eggs and 94.4% larvae, 44 days following infestation. Egg galleries were of similar length ($\bar{x}$ = 14.0 ± 1.2), to those established by overwintered brood adults in spring, 1984 (table 4, Exp. 1,3). However, the number of egg niches ($\bar{x}$ = 4.5 ± 0.9) established by parent adults that overwintered as larvae was nearly one-half that produced by overwintered adults. Production of a second brood by adults that overwintered as larvae was low. Only five gallery systems were discovered in bark samples on 13 September, 1984. A total of eight egg galleries (table 4, Exp. 3) contained only three eggs, 22 days following infestation.

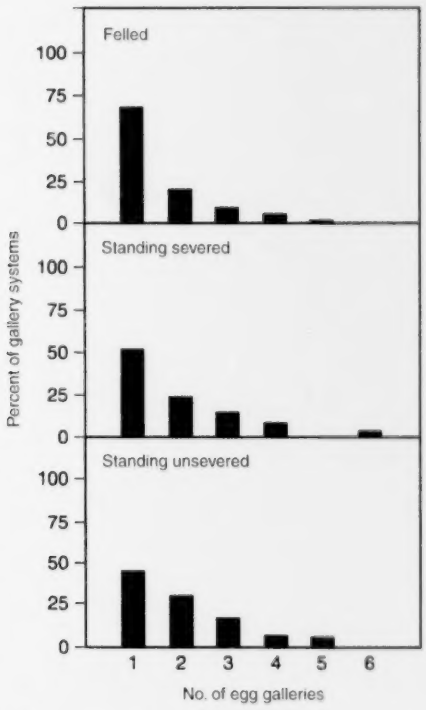

Fig. 5. *Proportion of gallery systems with 1 to 6 female egg galleries constructed in black spruce by* P. rufipennis, *spring 1983. Counts made on intact galleries from felled (N = 135), standing severed (N = 75) and standing unsevered (N = 74) trees*

3.1.3 Parent adult re-emergence

Re-emergence in 1983 from established gallery systems began ≈ 4–5 weeks following attack and peaked near mid-July (fig. 8). The number of beetles re-emerging then decreased rapidly until 12 August, after which no re-emergence occurred. In the laboratory, parent adults were capable of establishing a second brood, but there was little evidence for a third brood. Although re-emergence started later in 1984 than in 1983 the general patterns were similar to that in 1983 (fig. 8).

3.2 Host colonization under sun and shade

In 1983, attacks were first recorded on 14 June on one bole section exposed to full sunlight and on two sections in shade. Three weeks later, nine sections in shade, but only two exposed to full sunlight, had been successfully attacked. All logs in both sun and shade were infested with *P. rufipennis* by mid-August. Most were colonized all along the bole, from the cut base to as close as 2.5 cm

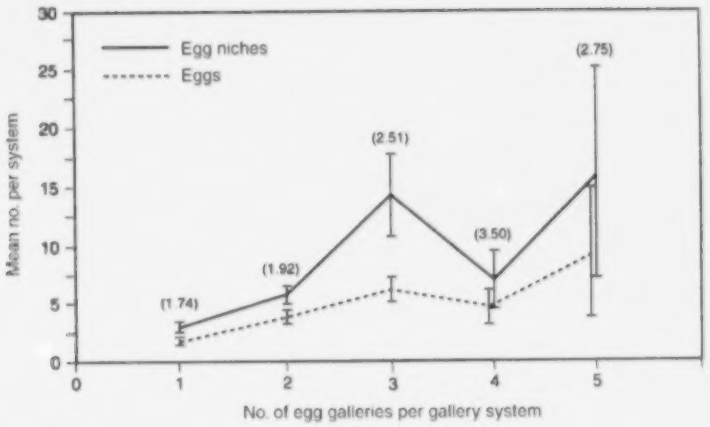

Fig. 6. *Relationship between mean numbers of egg niches and eggs and the number of egg galleries per gallery system. Numbers in parenthesis represent female to male sex ratios for 1, 2, 3, 4 and 5 gallery systems*

from the tip. Significantly higher numbers of gallery systems were established on logs in shade than in full sunlight (table 5). No significant differences due to position along the bole were apparent and the interaction of position and light exposure was also not significant. The number of adults remaining in the bark of trees exposed to shade was nearly double that found in trees exposed to full sunlight.

In 1984, light exposure and bole aspect interacted to influence gallery establishment (table 6). Few attacks were found on the upper aspect of logs exposed to full sunlight, whereas all aspects of logs felled in shade and the side and bottom of logs in full sunlight were successfully attacked. With the exception of the upper bole of logs exposed to sunlight, where few galleries were established, adult mortality was lower in trees under shade than in sunlight. No difference was observed between the mean lengths of egg galleries (mm) in the lateral aspects of logs exposed to full sunlight ($\bar{x} = 13.3 \pm 0.9$) and those in shaded logs ($\bar{x} = 15.1 \pm 1.0$).

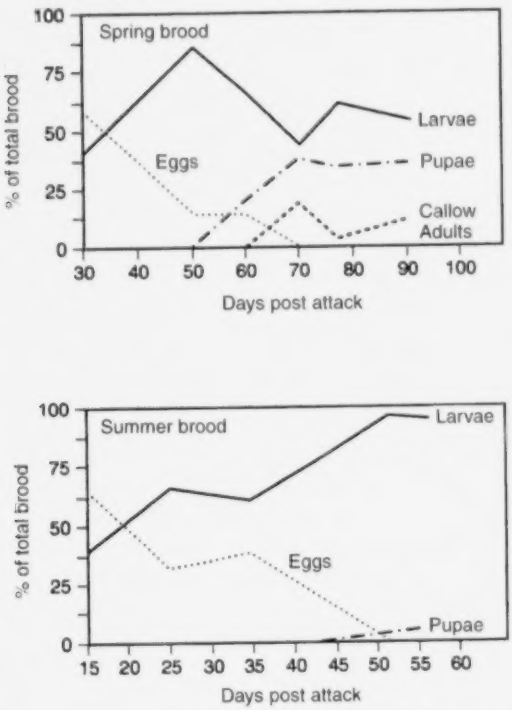

Fig. 7. *Seasonal life history of* P. rufipennis *on felled trees attacked in spring and summer, 1984. Proportions of life-stages throughout spring and summer determined from 7 trees attacked on 14 June and 4 trees attacked on 20 July, respectively*

3.3 Insect associates

In 1983, 461 *D. affaber* adults (9.6 per 100 cm^2) emerged from six black spruces, 70.3% within 2 m from the base of the tree. In 1984, 322 adults (5.0 per 100 cm^2) emerged from six black spruce trees, the majority again below 2 m. Emergence by *D. affaber* began on 23 May 1983, and peaked during the first two weeks of June, with a second smaller peak during mid-August when the study terminated (fig. 9). Over half of the adults had emerged by 1 July. In 1984, emergence began later than in 1983, but was otherwise similar (fig. 9). Emergence of *D. affaber* in the laboratory at room temperature was similar to that in the field, but the second peak occurred earlier and was not as pronounced as under field conditions.

In 1985, flight by *D. affaber* began on 12 June, peaked sharply, and was nearly over by the second week of July (fig. 10). During the first week the flight was comprised entirely of males. Females were first trapped on 19 June but the number of females captured in multiple funnel traps remained low with females comprising only 14.7% of the total catch.

In 1983, 828 *C. borealis* adults (17.3 per 100 cm^2) emerged from 6 trees, with 83.1% emerging at or below 3.5 m from the base. In 1984, 1179 adults (18.4 per 100 cm^2) emerged from six trees, again with the majority emerging at or below 3.5 m. Emergence by *C. borealis* began on 30 May 1983, peaked from 17 June to 15 July and had peaked by 18 August when the study terminated (fig. 11). In 1984, emergence was first observed on 21 June and was again bimodal, with peaks from 5 to 19 July and from 9 to 16 August (fig. 11). Only one *C. borealis* adult emerged from black spruce in the laboratory and none was captured in a multiple funnel trap.

Besides *P. rufipennis*, *D. affaber* and *C. borealis*, 343 other insects emerged from black spruce bolts held at

Table 4. *Mean length of female egg tunnels and number of egg niches produced by* P. rufipennis, *Newfoundland, 1984*

Exp. No.	Brood No.	Mean (+SE) Tunnel length (mm)	Egg niches	Egg niches per mm tunnel
Exp. I				
	First brood (N = 131)	16.1±0.5	8.1±0.3	0.5±0.01
	Second brood (N = 92)	16.9±0.8	4.6±0.9	0.5±0.02
	Third brood (N = 16)	8.9±1.4		0.4±0.06
Exp. II				
	Second brood (N = 30)	18.7±1.4	8.9±1.1	0.4±0.03
	Third brood (N = 10)	9.1±1.2	2.6±0.8	0.2±0.06
Exp. III				
	First brood (N = 25)	14.0±1.2	4.5±0.9	0.3±0.07
	Second brood (N = 8)	8.7±1.2	1.4±0.6	0.2±0.07

Table 5. *Colonization of felled black spruce exposed to full sunlight (N = 14) or dense shade (N = 15) by* P. rufipennis, *Newfoundland, 1983*

Exposure	Position	Bark thickness (mm)	Gallery systems No.	Gallery systems Mean±SE[a]	Adult brood ♂	Adult brood ♀	Adult brood Total	Dead adults No.	Dead adults %
Sun	Base	4.5±0.4	30	2.1±0.6	13	19	32	15	48.4
	Midbole	3.7±0.4	34	2.5±0.5	10	18	28	13	46.4
	Top	3.3±0.3	34	2.4±0.5	14	32	46	16	34.8
Shade	Base	4.8±0.4	67	4.5±0.7	13	65	78	16	20.8
	Midbole	4.0±0.4	67	4.5±0.8	24	58	82	23	28.0
	Top	3.0±0.3	46	4.2±0.7	10	57	67	23	33.9

[a]Significant difference in numbers of galleries between sun and shade exposure (ANOVA, P = 0.0003), but not between positions (P = 0.9687), or for interaction between position and exposure (P = 0.9139).

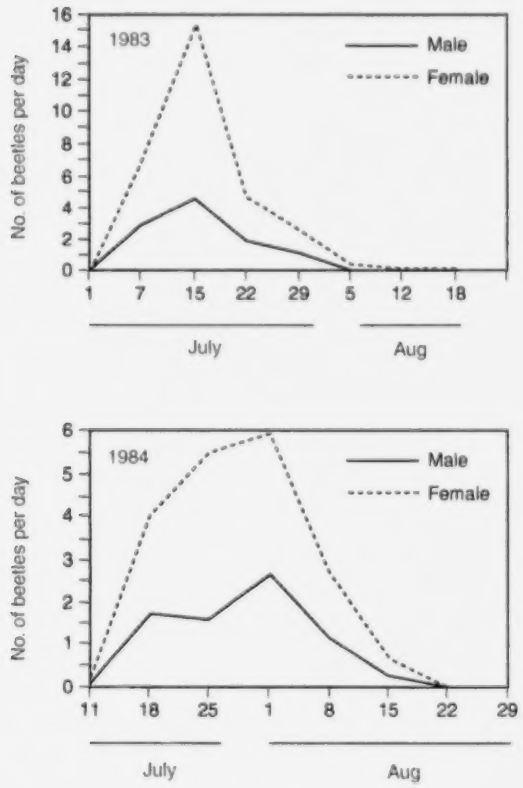

Fig. 8. *Re-emergence of* P. rufipennis *from black spruce in Newfoundland in 1983 and 1984*

room temperature in 1985. Of these, *Medetera* sp. (Diptera: Dolichopodiidae) and *Lasconotus intricatus* Kraus. (Coleoptera: Colydiidae), accounted for 70.9 and 12.8%, respectively. Additional coleoptera included 25 *Dryocoetes autographus* (Ratzeburg), 15 *Trypodendron lineatum* (Olivier) (Scolytidae), one *Thanasimus undulatus* (Say) (Cleridae), three *Ecphylus* sp., one *Eubazus* sp., one *Cosmophorus dendroctoni* Vier. (Hymenoptera: Braconidae), and two *Roptrocerus xylophagorum* (Ratzeburg) (Hymenoptera: Torymidae). Two staphylinid beetles, and several spiders were recovered but not further identified.

4 Discussion

4.1 Colonization sequence of *P. rufipennis*

Host colonization by *P. rufipennis* followed the typical host selection sequence of scolytids (WOOD, 1982; BORDEN, 1982). Discrete phases of colonization included emergence from the overwintering site in black spruce bark, dispersal, and selection and establishment on felled and standing trees.

4.1.1 Overwintering site and stadia

Unlike some bark beetles (CHAMBERLIN, 1958; THOMAS, 1961), *P. rufipennis* spent the winter in the bark rather than in the duff. Low winter temperatures can cause substantial mortality in bark beetles, e.g. the spruce beetle, *Dendroctonus rufipennis* (Kirby) (MASSEY and WYGANT, 1954; TERRELL, 1954; FRYE et al., 1974), and probably caused the reduction in survival of *P. rufi-*

Table 6. *Colonization of felled black spruce exposed to full sunlight (N = 10) or dense shade (N = 10) by* P. rufipennis, *Newfoundland, 1984*

Exposure	Aspect	Bark thickness (mm)	Gallery systems No.	Gallery systems Mean ± SE[a]	Adult brood ♂♂	Adult brood ♀♀	Adult brood Total	Dead adults No.	Dead adults %
Sun	Upper	3.6 ± 0.1	4	0.4 ± 0.2	0	1	1	0	—
	Side	3.4 ± 0.2	51	5.1 ± 0.9	18	41	59	8	13.6
	Bottom	3.6 ± 0.1	77	7.7 ± 0.6	16	64	80	67.5	7.5
Shade	Upper	3.7 ± 0.1	66	6.6 ± 0.5	28	117	145	6	4.1
	Side	3.6 ± 0.1	54	5.4 ± 0.6	32	112	144	5	3.5
	Bottom	3.7 ± 0.1	46	4.6 ± 0.9	30	92	122	6	5.0

[a]Significant difference in numbers of galleries between sun and shade exposure (ANOVA, P = 0.0364), between aspects (P = 0.0005), or for interaction between aspect and exposure (P = 0.0001).

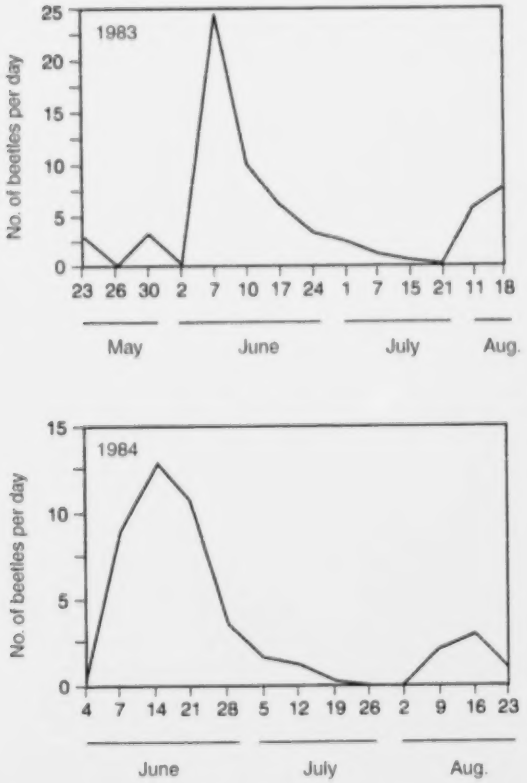

Fig. 9. *Seasonal emergence of* D. affaber *from black spruce in Newfoundland in 1983 and 1984*

pennis brood adults in felled and standing severed trees during the winter in Newfoundland. The low survival in cut trees may have been caused by desiccation of their bark tissue. Overwintering as an adult offers an advantage in northern climes, because reproduction can commence immediately after temperatures warm up in spring, enhancing the opportunity for a second brood. Although the number of beetles that overwintered below 0.5 m on the bole of black spruce was not investigated, hibernation near the root collar might have high survival value for *P. rufipennis*, because of protection from low temperatures and woodpecker predation under a snow cover.

4.1.2 Host selection, attack and brood establishment

The short interval between girdling of trees and arrival by *P. rufipennis* implies that adults may respond to host odours to locate a suitable breeding substrate. Several species of scolytids exploit host volatiles (Chapman, 1962), most notably ethanol (Moeck, 1981) to locate suitable breeding material. However, such primary attraction is confounded by pheromones released by early attacking beetles. Furthermore, the time interval between cutting and first attack on felled trees was fairly long, suggesting that visual orientation may also be important in host selection. This hypothesis is consistent with observations that *P. rufipennis* is not capable of orienting to weakened hosts through olfaction alone (Gara and Holsten, 1975).

The doubled attack density on felled over standing severed trees, and the finding that only two standing unsevered trees were attacked, supports the hypothesis that *P. rufipennis* is a secondary bark beetle on black spruce and requires some means of host predisposition for establishment and optimal reproduction. Moreover, the rate of increase on standing unsevered trees was slower than on felled and standing severed trees, possibly due to a greater level of tree resistance.

In Maine, Hosking and Knight (1975) compared window trap catches from three heights on the bole, and reported highest numbers attacking at 7.5 m. In Newfoundland, *P. rufipennis* almost always attacked in the lower bole first, and only after mass attack were trees attacked higher on the bole. The lack of a significant relationship between attack density and sample height or bark thickness is surprising. For many species, significant relationships exist between densities of attack or beetle brood and parameters such as tree height and bark thickness (Shepherd, 1965; Amman, 1969, 1972a; Coulson et al., 1976; Haack et al., 1984; Amman and Pasek, 1986). Possibly, by dispersing evenly over the bole, *P. rufipennis* can fully utilize the host resource, and can avoid excessive competition from con- and hetero-specifics, and can lessen the chance of parasitism by not concentrating in areas of bark where levels of parasitoid-attracting kairomones might be high.

There has been disagreement over which sex of *P. rufipennis* initiates attack (Hopkins 1899; Blackman and Stage, 1918; Simpson, 1929; Hilton, 1968; Rudinsky et al., 1978). Our observations that the male usu-

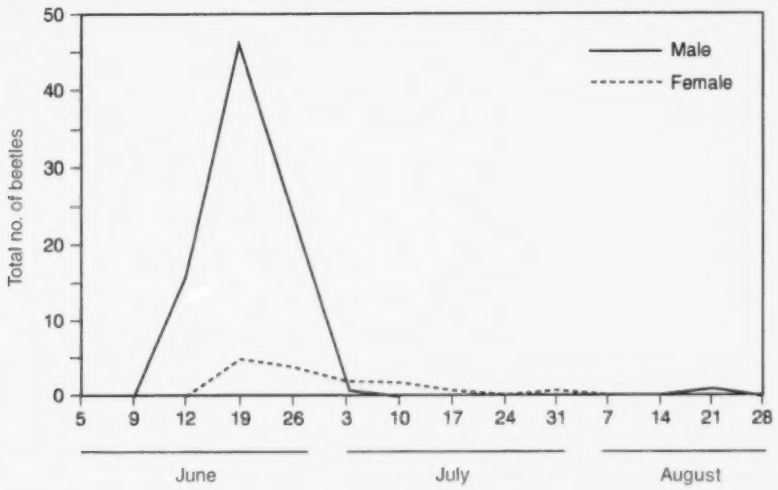

Fig. 10. Seasonal flight pattern of D. affaber *, Badger, Newfoundland, 1985*

ally initiates the attack and excavates the nuptial chamber is in agreement with the trend for most harem polygynous taxa. Aggregation pheromones are almost invariably produced by the initiating sex, a phenomenon that was confirmed for *P. rufipennis* (Bowers and Borden, 1990; Bowers et al., 1991). The habit of male *P. rufipennis* remaining with the females after copulation and guarding the entrance hole is common in polygynous bark beetles. This behaviour was interpreted by Kirkendall (1983) as 'resource defense'; males who guard reproducing females after mating probably derive a net benefit over those who leave the resource early and risk loss of sperm through ejaculate competition or loss of brood to predators.

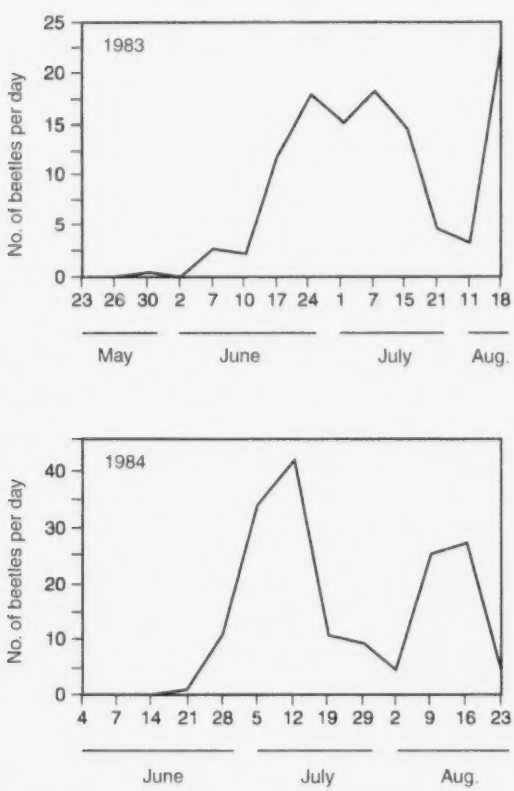

Fig. 11. Seasonal emergence of C. borealis *from black spruce in Newfoundland in 1983 and 1984*

The increase in female to male sex ratio as the number of female galleries per gallery system increases (fig. 6), confirms that the number of egg galleries is a reliable indicator of the number of females per male, and therefore can be considered a measure of male reproductive success. However, variation in harem size may also be the result of differences in resource quality (Kirkendall, 1983). Our results also indicate that as males acquire more females, each female generally produces more eggs, a second measure of reproductive success (fig. 6). Blackman and Stage (1918) found the opposite result for *P. rufipennis* on larch, suggesting that black spruce is a better host.

Although egg gallery length increased linearly during the first 5 weeks of spring 1983 the majority of the variation in gallery length remains unexplained. Possibly there is an uneven decline in the amount or quality of phloem tissue over time; individual gallery systems may also be prone to different levels of intraspecific competition. Significant correlations between the number of eggs and length of female galleries in both spring and summer broods support the hypothesis that such factors may limit *P. rufipennis* success in black spruce. Although a significant association existed between number of eggs and number of egg niches for both spring and summer broods, the high degree of scatter suggests that counts of egg niches may not be a reliable measure of female fecundity since some females appear to excavate egg niches but fail to oviposit.

Our findings support those of Simpson (1929) that *P. rufipennis* is univoltine, but may have up to three broods per year. In Newfoundland, *P. rufipennis* established at least two broods per year. Pupae of the first brood developed into callow adults late in the season, and did not emerge until the following spring. The second (summer) brood, overwintered primarily as larvae (fig. 7), although a few individuals could have reached adulthood before winter. Parents artificially removed from second brood trees were capable of establishing new galleries with very few eggs and larvae in fall, 1984.

Therefore, a third brood is considered likely only under the most favourable conditions. SIMPSON (1929) reported that where *P. rufipennis* produces a third brood, the third brood progeny hibernate as larvae for two winters.

4.1.3 Parent adult re-emergence

The question as to why beetles re-emerge is intriguing. A nutrient deficiency may occur after a period of feeding in the fungus-infested tissue, and required nutrients may only be available from a new host. Similarly, re-emergence may avoid deteriorating bark that could contribute to mortality from pathogenic organisms such as fungi, nematodes and mites. Finally, parent adults may re-emerge to avoid overcrowding (ANDERBRANT, 1985). In Newfoundland, the total time from egg to callow adult was estimated to be ≈ 60 days, as compared with 40 days in New Brunswick (SWAINE, 1929), probably because of cooler summer temperatures in Newfoundland.

4.2 Host colonization under sun and shade

Our results agree with those of PRICE (1966), who reported that the upper aspects of red spruce logs were not attacked by *P. rufipennis*, and most attacks occurred on the lower aspects protected from direct sunlight. Subcortical temperature and moisture affect the development and survival of most bark beetles (GAUMER and GARA, 1967; SCHMID, 1981), and gallery construction may proceed only as long as moisture and temperature conditions are suitable (REID, 1962). The preference by *P. rufipennis* for trees in shade, or the shaded portions of trees in sun, reflects a strong influence of bark temperature and moisture. Because black spruce bark is relatively thin, especially on small diameter trees, the rate of desiccation in sun was much faster than in shade. In laboratory experiments, brood success of *P. rufipennis* on white spruce was also reduced as bark moisture levels decreased (BEANLANDS, 1967).

4.3 Insect associates

The sequence of emergence and arrival of *D. affaber* and *C. borealis*, to trees attacked by *P. rufipennis*, followed a characteristic temporal pattern. In the field and laboratory, emergence of *D. affaber* coincided with that of *P. rufipennis*, but on only a few trees did *D. affaber* attack before *P. rufipennis*. It is probable that the less aggressive *D. affaber* exploits hosts that have been weakened by *P. rufipennis*. As is common in the Scolytidae (RANKIN and BORDEN, 1991) the two species apparently compete for resources because galleries of both species often occur adjacent to each other and may intersect. Peak emergence of *C. borealis* occurred approximately 3 weeks later than for *P. rufipennis* and *D. affaber*, reflecting the need to utilize the entrance holes and galleries of other insects to gain entry into bark after which they excavate their own galleries by mining perpendicularly to the main gallery (CHAMBERLIN, 1939; BRIGHT, 1976; WOOD, 1982). Although the frequency of *C. borealis* adults and larval mines in gallery systems established by *P. rufipennis* and *D. affaber* suggested exploitative competition, their small size precluded comparative assessment of brood establishment and development.

The cylindrical bark beetle, *L. intricatus* was a frequently found representative of the numerous associates of *P. rufipennis* (HILTON, 1968). The full impact of cylindrical bark beetles on scolytid populations has not been elucidated but they may prey on immature beetles. The response by this species to the aggregation pheromone of *P. rufipennis* (BOWERS and BORDEN, 1992) is consistent with this hypothesis. *Medetera* spp. are also known predators of bark beetle eggs and larvae (SCHMID, 1971). Because *Medetera* sp. comprised 70.9% of the total associates that emerged from black spruce bolts it may have a significant impact on populations of the four-eyed spruce bark beetle, as hypothesized by BLACKMAN and STAGE (1918). Unidentified clerid larvae were frequently encountered during dissection of bark samples in 1983, reflecting their importance as predators of bark beetles (CHAMBERLIN, 1939; AMMAN, 1972b; BERISFORD, 1980). The incidence of four species of hymenopterous parasitoids in black spruce infested with *P. rufipennis* is noteworthy. Some or all of *Ecphylus* sp., *R. xylophagorum*, *Eubazus* sp., and *C. dendroctoni* may be effective in reducing populations of the beetle.

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Authors' addresses: W. W. Bowers (for correspondence), A. Raske, Canadian Forest Service, Newfoundland and Labrador Region, PO Box 6028, St. John's, Newfoundland, Canada A1C 5X8; J. H. Borden, Centre for Pest Management, Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia, Canada V5A 1S6